A Long-Snouted Predatory Dinosaur from Africa and the Evolution of Spinosaurus


Fossils discovered in Lower Cretaceous (Aptian) rocks in the Ténéré Desert of central Niger provide new information about spinosaurids, a peculiar group of piscivorous theropod dinosaurs. The remains, which represent a new genus and species, reveal the extreme elongation and transverse compression of the spinosaurid snout. The postcranial bones include blade-shaped vertebral spines that form a low sail over the hips. Phylogenetic analysis suggests that the enlarged thumb claw and robust forelimb evolved during the Jurassic, before the elongated snout and other fish-eating adaptations in the skull. The close phylogenetic relationship between the new African spinosaurid and Baryonyx from Europe provides evidence of dispersal across the Tethys seaway during the Early Cretaceous.

In 1912, a series of extremely high-spined vertebrae and a peculiar lower jaw with subconical crocodilike teeth were discovered in the Bahariya oasis in central Egypt (1). These fossils provided evidence that a large, piscivorous, sail-backed predator roamed the northern shores of Africa during the Late Cretaceous (Cenomanian). This partial skeleton, *Spinosaurus aegyptiacus,* was destroyed during World War II, and few remains that are attributable to this taxon have since been recovered in these horizons (2–5).

Additional bones of *Spinosaurus*-like predators have been discovered in Lower Cretaceous (Aptian or Albian) deposits in Niger and Brazil and in somewhat older (Barremian) rocks in Europe. The Nigerien fossils include peculiar arched snout tips and enormous manual unguals (6–8); the Brazilian remains consist of a single partial skull, *Irritator* (9, 10); and the European fossils, *Baryonyx,* include the first relatively complete spinosaurid skeleton (11–13).

Fossils were recovered recently from the Elrhaz Formation in Niger (Fig. 1). These Aptian-age rocks consist predominantly of fluvial channel deposits and are exposed in low outcrops amid dune fields in the Ténéré Desert (6, 14). The fossils found here include plant, invertebrate, and vertebrate remains; the vertebrate remains consist mainly of disarticulated bones and teeth in basal channel lag deposits. Dinosaurs are represented by at least three theropods, two sauropods, and three ornithopods (15).

The newly discovered fossils include a partial skull and a skeleton of a new spinosaurid, *Suchomimus tenerensis* gen. nov. sp. nov. (16), which can be distinguished from other spinosaurids (17). An articulated snout (Fig. 2A and B) reveals its remarkably long, low, and narrow proportions. The elongation of the snout is the result of the hypertrophy of both the premaxilla and the anterior ramus of the maxilla. The premaxillae, which fuse early in growth, each contain alveoli for seven teeth. The subconical crowns are slightly recurved and have fine marginal serrations and textured enamel surfaces (Fig. 2E). The external nares are retracted posterior to the premaxillae (18). As in *Baryonyx,* the quadrate foramen is very large, and the distal condyles are very broad.

In the postcranial skeleton, the cervical series arches upward (18) and has prominent epipophyses for muscle attachments. The neural spines increase in height rapidly in the middorsal vertebrae, forming a low median sail that is deepest over the sacral vertebrae (Fig. 3). This vertebral morphology, incidentally developed in *Baryonyx* (13), is distinct...
from that in *Spinosaurus* (1), in which the much deeper sail arches to an apex over the middorsal vertebrae (Fig. 4B).

Complete pectoral and pelvic bones show a deep subrectangular acromion on the scapula and a low obturator flange on the ischium. The distal end of the pubis is distinctive. Although there is a short, sagittal, symphyseal flange that may correspond with the pubic foot in other theropods, the flattened, subrectangular distal end of the pubis faces anteriorly, perpendicular to the sagittal plane (Fig. 3). The forearm is remarkably stout, and manual digit III is robust, as seen in the size of metacarpal III and the third ungual (Fig. 3 and Table 1). The femur has a blade-shaped anterior trochanter, and the ascending process of the astragalus is taller than that in *Allosaurus* (20).

Phylogenetic analysis (21, 22) links spinosaurids with torvosaurids (23) and places this clade (Spinosauridae) as the sister group to Neotetanurae (Fig. 4A and Table 2). The derived features that are shared between spinosaurids and torvosaurids, including the short forearm and the enlarged manual digit I ungual (22), appear to have evolved by the Middle Jurassic (Fig. 4B). A hook-shaped coracoid characterizes *Suchomimus*, *Baryonyx*, and neotetanurans but not torvosaurids (24). Thus, the hook-shaped coracoid either evolved convergently in neotetanurans and spinosaurids or originated as a tetanuran synapomorphy that was subsequently lost in torvosaurids (21, 22).

Spinosaurids are characterized by numerous derived features, many of which are related to piscivory [including an unusually long snout with a long secondary palate; a terminal rosette of teeth in the upper and lower jaws (25); subcylindrical, spaced crowns; posteriorly displaced external nares; ventrally positioned basipterygoid articulation; and other features (8, 13, 22)]. Our analysis suggests that spinosaurids can be divided into two clades, the Baryonychinae...
and the Spinosaurinae (26), which diverged before the Barremian (Fig. 4B). The baryonychines Suchominus and Baryonyx are distinct (16, 27) but closely related, as evidenced by several derived features that include the small size and increased number of dentary teeth posterior to the terminal rosette and the deeply keeled anterior dorsal vertebrae (22).

Many other similarities between these two taxa are ambiguous because they are not preserved in other spinosaurids. The spinosaurines Irritator and Spinosaurus are united on the basis of the straight unserrated crowns, the small first premaxillary tooth (4, 8), and the increased spacing of the teeth in the upper and lower jaws (8, 13, 22) (Fig. 4B). The posterior displacement of the external nares in Irritator (9) and the deep sail in Spinosaurus (Fig. 4B) may eventually characterize the Spinosaurinae, but these features are currently known in only one member.

Table 1. Length measurements (millimeters) and ratios in Suchomimus tenerensis (MNN GDF500), Baryonyx walkeri (13), and Allosaurus fragilis (20). Unguals are measured perpendicular to the articular end. Question mark indicates lack of preservation; I, II, and III are unguals of manual digits I, II, and III, respectively.

<table>
<thead>
<tr>
<th>Bone</th>
<th>Suchomimus</th>
<th>Baryonyx</th>
<th>Allosaurus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humerus</td>
<td>560</td>
<td>483*</td>
<td>310</td>
</tr>
<tr>
<td>Radius</td>
<td>255</td>
<td>225</td>
<td>222</td>
</tr>
<tr>
<td>Metacarpal III</td>
<td>130</td>
<td>?</td>
<td>101</td>
</tr>
<tr>
<td>I</td>
<td>190</td>
<td>173*</td>
<td>102</td>
</tr>
<tr>
<td>II</td>
<td>165</td>
<td>?</td>
<td>92</td>
</tr>
<tr>
<td>III</td>
<td>120</td>
<td>120*</td>
<td>54</td>
</tr>
<tr>
<td>Femur</td>
<td>1075</td>
<td>?</td>
<td>850</td>
</tr>
<tr>
<td>Tibia</td>
<td>945</td>
<td>?</td>
<td>690</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Ratios</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Radius/humerus</td>
<td>0.46</td>
<td>0.47</td>
<td>0.72</td>
</tr>
<tr>
<td>I/radius</td>
<td>0.75</td>
<td>0.77</td>
<td>0.46</td>
</tr>
<tr>
<td>II/I</td>
<td>0.87</td>
<td>?</td>
<td>0.90</td>
</tr>
<tr>
<td>III/I</td>
<td>0.63</td>
<td>0.69</td>
<td>0.53</td>
</tr>
<tr>
<td>Tibia/femur</td>
<td>0.88</td>
<td>?</td>
<td>0.81</td>
</tr>
</tbody>
</table>

*This measurement was taken by the authors and differs slightly from that reported previously (13).
Before the discovery of Suchomimus, the geographic distribution and relationships of spinosaurids matched the general pattern of continental fragmentation during the latter half of the Mesozoic and thus could be explained by large-scale vicariance. The split between the northern Baryonyx and the southern spinosaurines, in this hypothesis, could be attributed to the opening of the Tethyan seaway between Laurasia and Gondwanaland, and the divergence among spinosaurines could be the result of the subsequent opening of the Atlantic Ocean between South America and Africa. The discovery of Suchomimus on Africa in the mid-Cretaceous, however, complicates this scenario. Its closest relative is the European Baryonyx rather than the African Spinosaurus—a pattern of relationships that is inconsistent with the large-scale sequence of continental rifting described above.

One biogeographic hypothesis accounts most parsimoniously for the distribution of the four spinosaurids (28), assuming that we have correctly ascertained their phylogenetic relationships and accept the rifting sequence between the continental areas outlined above. Initially, spinosaurids may have had a distribution across Pangaea that was split by the opening of the Tethys; baryonychines evolved to the north (Europe, or Laurasia), and spinosaurines evolved on the southern landmass (South America and Africa, or Gondwanaland). A single dispersal event from Europe to Africa during the Early Cretaceous would account for the presence of Suchomimus in Africa. Alternative scenarios involve additional dispersal or extinction events to account for recorded distributions. The phylogenetic and biogeographic relationships of Suchomimus and other spinosaurids provide further evidence of dispersal across the Tethyan seaway during the Early Cretaceous (21, 29).

Table 2. Character-state matrix for two outgroups (Ceratosauria and Neotetanurae), six ingroups, and 45 characters (22) used in a phylogenetic analysis of spinosaurids (Fig. 4A). The holotypic specimens of Angaturama and Irritator were scored as one taxon (Irritator). X, unknown as a result of transformation; ?, not preserved.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>10</th>
<th>20</th>
<th>30</th>
<th>40</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ceratosaurus</td>
<td>0000</td>
<td>0000</td>
<td>0000</td>
<td>0000</td>
</tr>
<tr>
<td>Neotetanurae</td>
<td>0000</td>
<td>0000</td>
<td>0000</td>
<td>0000</td>
</tr>
<tr>
<td>Eustreptospondylus</td>
<td>11111</td>
<td>00000</td>
<td>00000</td>
<td>00011</td>
</tr>
<tr>
<td>Torvosaurus</td>
<td>11111</td>
<td>11111</td>
<td>11111</td>
<td>11111</td>
</tr>
<tr>
<td>Baryonyx</td>
<td>11111</td>
<td>11111</td>
<td>11111</td>
<td>11111</td>
</tr>
<tr>
<td>Suchomimus</td>
<td>11111</td>
<td>11111</td>
<td>11111</td>
<td>11111</td>
</tr>
<tr>
<td>Irritator</td>
<td>11111</td>
<td>11111</td>
<td>11111</td>
<td>11111</td>
</tr>
<tr>
<td>Spinosaurus</td>
<td>11111</td>
<td>11111</td>
<td>11111</td>
<td>11111</td>
</tr>
</tbody>
</table>


The holotypic skeleton of Spinosaurus aegypticus includes subconical teeth, dentaries with a squared distal end, and high-spined dorsal vertebrae (7); the association of these characters is confirmed by additional remains from Morocco (3) and Algeria (4). Although the Moroccan and Algerian materials have been referred to a different species (S. maroccana), its distinction from S. aegypticus (by the proportions of the centrum of an isolated cervical vertebra) and the basis for the referral of additional material are questionable. We regard S. maroccana as a nomen dubium and provisionally refer all spinosaurid material from African and Ceranomanian-age rocks in northern Africa to S. aegypticus. Storzer (30) described other postcranial remains from the Bahariya oasis as “Spinosaur B,” but these can be shown to overlap with a partial skeleton of the allosauroid Carcachodontosaurus saharicus from the same locality (21). Recently a new genus and species, Sigilmassaurus brevicolli, was erected on the basis of isolated vertebrae from Ceranomanian-age rocks in Morocco (3). We question its distinction from C. saharicus (by proportions of the centrum of an isolated cervical vertebra). We regard Sigilmassaurus brevicolli as a subjective junior synonym of C. saharicus, to which we provisionally refer all carcachodontosaurid material from African and Ceranomanian-age rocks in northern Africa.


11. Shortly after Irritator challengeri was described (9), the anterior end of a spinosaurid snout was described from the same deposit as Angaturama limai (8), which may well pertain to the same taxon or possibly to an as yet indeterminate spinosaurid (8–10). We regard the bones that were identified as the left postorbital, left jugal, right atlantal neural arch, and left angular, respectively. These are reposited accordingly in our cranial reconstruction (Fig. 2, A and D). The plate-shaped anteromedial process of the postorbital, left jugal, right atlantal neural arch, and left angular (13) as the posterior portion of the right surangular, right praearticular, central body of the left pterygoid, and right angular, respectively. These are reposited accordingly in our cranial reconstruction (Fig. 2, C and D). The plate-shaped anteromedial process of the maxilla was formerly identified as the vomer (13). We regard the deeper proportions of the occiput as reconstructed in B, weakened by an apparent intramembranous ventral displacement of the cranium. The cranium in Baryonyx was probably as low, long, and narrow as in

References and Notes


14. The Tagma Group is composed of terrestrial rocks of middle to late Cretaceous age. Three formations (Tassili, Elrhaz, and Eckhar) have been recognized [H. Faure, Mem. B.R.G.M. Paris 47, 1 (1966); J. Creighton and R. Pouget, ibid. 48, 1 (1967)]. In the region southeast of the Air highlands, the Tagma Group was divided into eight Gadoufaoua (GAD) ages by the Center for Atomic Energy [E. Molina, Rapp. C.E.A. Marseille 1965, 1 (1965)]. Horizons corresponding to GAD 5 have yielded all of the fossils in the present report and those described previously (Fig. 1). GAD 5 appears to include the upper part of the Eckhar Formation and the lower part of the Eckhar Formation (6).

15. Theropods include the spinosaurid described here, an indeterminate tetanuran known primarily from teeth, and a small basal coelurosaur. Currently, there is no evidence to support the previous referral of small theropod remains from Gadoufaoua to Elaphrosaurus iguanodon (6) [A. F. de Lapparent, Mem. Soc. Geol. Fr. 88A, 1 (1966)]. Sauropterygia include a common, high-spined basal diplodocoid [formerly referred to as a dicraeosaurine (7)] and a rare titanosaur. Ornithopods include the dryosaurid Valdosaurus nigeriensis [P. M. Galton and P. Taquet, Geobios 15, 147 (1982)], the common “guanodo trapu” [S. Chablis, thesis, Universite de Paris (1988)], and the high-spined Ouranosaurus nigeriensis (6). Nondinosaurian vertebrates that were not previously recorded include a long-snouted basilosaurid and an azhdarchid pterosaur.

16. Etymology: Souchos, crocodile [Greek]; imos, mimic [Greek]; tenere, Tenere Desert; ensis, from (Latin). Named for the low elongate snout and piscivorous adaptations of the jaws and for the region of the Sahara in which it was discovered. Holotype: Partial disarticulated skeleton (MNN GFDF050) cataloged in the collections of the Musee National du Niger (MNN), Niamey, Republic of Niger. Referenced material: Articulated premaxilla (MNN GFDF051), right mandible (MNN GFDF052), partial dentaries (MNN GFDF053, GFDF054, and GFDF055), axis (MNN GFDF056), posterior cervical vertebra (MNN GFDF057), two caudal vertebrae (MNN GFDF10 and GFDF11), and many additional bones and teeth. Diagnosis: Spinosaurid characterized by an elongate posteroventral maxillary process that nearly excludes the maxilla from the external naris; broadened posterior dorsal, sacral, and anterior caudal neural spines; robust humeral tuberosities; hypertrophied ulnar olecranon process that is offset from the medial articulation; and hook-shaped radial ectepicondyle.

17. In contrast to the specimens described here, previously known spinosaurid material from Niger has been limited to fragmentary disarticulated bones that are attributable to an as yet indeterminate spinosaurid (6–8). Recently, however, a new spinosaurid, Crétatitansaurus lapparenti, was named on the basis of material from Gadoufaoua (4). The holotypic specimen consists of portions of the premaxilla, maxilla, and dentary, the association of which was not established. The authors state that the material differs from Baryonyx by the “brevirostrine condition of premaxilla” [H. Assheton and P. M. Galton, Mem. Soc. Geol. Fr. 88A, 1 (1966)]. However, no distinguishing features or proportions are apparent to us or to previous authors (13), who attributed the premaxillae to an indeterminable species of Baryonyx. We therefore regard C. lapparenti as a nomen dubium.

18. We offer alternative identifications for several cranial elements in the holotypic specimen of Baryonyx walker. We regard the bones that were identified as the left postorbital, left jugal, right atlantal neural arch, and left angular (13) as the posterior portion of the right surangular, right prearticular, central body of the left pterygoid, and right angular, respectively. These are reposited accordingly in our cranial reconstruction (Fig. 2, C and D). The plate-shaped anteromedial process of the maxilla was formerly identified as the vomer (13). We regard the deeper proportions of the occiput as reconstructed in B, weakened by an apparent intramembranous ventral displacement of the cranium. The cranium in Baryonyx was probably as low, long, and narrow as in
Suchomimus. The cervical series in both Baryonyx and Suchomimus shows a dorsal offset of the anterior articulations.

22. The following 45 synapomorphies (optimized with de-

20. C. W. Gilmore, Bull. U.S. Natl. Mus. 19. E. Buffetaut, Rev. Mus. La Plata or smaller (1) than the orbit; than three times the length of the antorbital fenestra; form: convergent (0); expanded into a premaxillary/antorbital laminae: present (0); absent (1); anterior to (1) the anterior margin of the maxilla; paradental laminae: present (0); absent (1); large (1); size: moderate to large (0); reduced to a small ßange (1).

26. Baryonychinae (Suchomimus and Bary-

27. Revised diagnosis for Baryonyx walkeri: Spinosaurid characterized by fused nasals with a median crest terminating posteriorly in a cruciate process, a solid subrectangular lacrimal horn, a marked transverse constriction of the sacral or anterior caudal centra, a well-formed peg-and-notch articulation between the scapula and coracoid, an everted distal margin of the pubic blade, and a very shallow ﬁbular fossa.

28. Biogeographic hypotheses were optimized with dis-

34. Supported by the David and Lucile Packard Foundation, National Geographic Society, Pritzker Foundation, and the Women’s Board of the University of Chicago. We thank K. Bainbridge, A. Boldizsar, J. Bradshaw, J.-P. Cavigelli, J. Ogradnick, and F. Stroik for participation in ﬁeld excavation; C. Abzacrina for drawing from the original specimens and executing the ßnal drafts of Figs. 1A and 2 through 4; B. Strack (Field Museum) for assistance with microphotography; Q. Cao and E. Dong for directing fossil preparation and casting; and J. Hopson, F. Landis, B. Molnar, and H.-D. Sues for reviewing an earlier draft of the paper. We gratefully acknowledge the assistance of I. Kouda of the Ministère de l’Enseignement Supérieur de la Recherche et de la Technologie (Niger). For permission to conduct ﬁeldwork, we are indebted to the Republic of Niger.

31 August 1998; accepted 2 October 1998

Ultrasable Mesostructured Silica Vesicles
Seong Su Kim, Wenzhong Zhang, Thomas J. Pinnavaia*

A family of mesoporous molecular sieves (denoted MSU–G) with vesiclelike hierarchical structures and unprecedented thermal (1000°C) and hydrothermal stabilities (more than 150 hours at 100°C) associated with high SiO2, cross-linking was prepared through a supramolecular assembly pathway that relies on hydrogen bonding between electrically neutral gemini surfactants of the type C12H25–NH(CH2)3+NH2 and silica precursors derived from tetraethy-orthosilicate. The vesicle shells are constructed of one or more undulated silica sheets that are about 3 nanometers thick with mesopores (average diameters from 2.7 to 4.0 nanometers) running both parallel and orthogonal to the silica sheets, which makes the framework structure bicontinuous and highly accessible. Catalytic metal ion centers [for example, Ti(V) and Al(III)] have been incorporated into the framework with the retention of hierarchical structure.

Substantial progress has been made recently in extending the supramolecular assembly of mesostructured inorganic frameworks to include hierarchical forms with a variety of particle shapes (1–3). Mesoporous metal oxide molecular sieves with vesiclelike morphologies are of interest as potential catalysts and sorbents, in part because the mesostructured shells and intrinsic textural pores of the vesicles should efﬁciently transport guest species to framework binding sites. However, all vesicle-like mesostructures reported to date had shells of undesirable thickness. More important, like many mesoporous molecular sieves with conventional particle morphologies, the framework structures deﬁning the vesicle shells were lacking in structural stability. For instance, a vesicular aluminophosphate with mesoscale d spacing and surface patterns that mimicked diatom and radiolarian skeletons collapsed to AlPO4–crystobalite with a complete loss of the hierarchical patterns at 300°C (4). Also, vesiclelike siliconic acid polymers that were structured by a didodecyldimethylammonium bromide template lost their hierarchical structures when washed with alcohols (5). Macroscopic hollow spheres of mesoporous MCM-41 (2, 6) have been prepared from oil-in-water emulsions, but